Mathematics, 1919, as a consequence of a misprint in my "second report on recent progress in the theory of groups of finite order," *Bull. Amer. Math. Soc.*, **9**, 1903, p. 118.

PHOTIC ORIENTATION IN INSECTS

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The idea that orientation in organisms is dependent upon the relation in the physical and chemical states produced by the stimulating agent in symmetrically located receptors and the relation in the activity of the locomotor apparatus on opposite sides is widely accepted. This idea extends back to the botanist, Ray (1693), it was applied to lower animals by Verworn in 1894 and to higher animals including insects by Bohn in 1904 and Loeb in 1906. It has been referred to as the difference of intensity theory, the continuous action theory, the tropism theory, the Verworn theory, the Ray-Verworn or DeCandolle theory, the muscle-tension theory and Loeb's muscle-tension theory. We shall call it the Ray-Verworn theory.

Referring to insects, Bohn, Loeb, Garrey and others maintain that light affects the tonus of the muscles in proportion to the intensity of the illumination of the receptors with which they are connected and in such a way that when the eyes on opposite sides are unequally illuminated, the legs on one side move faster than those on the other resulting in turning until the eyes are equally illuminated, when the tonus of the legs on opposite sides becomes equal and the turning ceases. These authors maintain that whenever insects are oriented, the receptors on opposite sides receive the same amount of stimulating energy. They hold that orientation is the result of balanced action in the two halves of the body.

There are numerous reactions involved in the process of orientation of insects and other animals which are not in accord with these views. Some of these follow.

If one eye of the drone-fly, Eristalis tenax, is covered it deflects strongly toward the functional eye making circus movements, but after a certain time it orients fairly accurately, especially in a well defined beam of light. Similar results have been obtained in observations on various other insects by Radl, (1903), Holmes (1905), Carpenter, (1908), Dolley (1916), and Minnich (1919). The eyes on opposite sides are not equally stimu-

lated when these insects with but one functional eye are oriented as is demanded by the Ray-Verworn theory. And the same may be said in reference to the fiddler-crab and a number of other forms that move sidewise toward the light.

In the robber-fly, Erax rufibarbis, with one eye covered the body assumes a tilted posture. The legs on the blind side are much more extended than those on the normal side and the feet consequently tend to move faster on the former than on the latter side, resulting in turning toward the normal side. Similar reactions are obtained if the lower half of one eye, the right e.g., and the upper half of the other eye are covered, i.e. they lean toward the right side and turn to the right; but if such specimens are laterally illuminated from the left, they will, under certain circumstances, turn to the left. Thus they turn toward the side on which the extension of the legs is greater, and in the direction precisely opposite to that which would obtain if it were in accord with the tonus hypothesis.

If Eristalis on the wing is illuminated from above or below it turns directly upward or downward. This turning can not be due to unequal illumination of the two eyes in accord with the Ray-Verworn theory for the two eyes may be continuously equally illuminated. Similar responses have been observed in Caprella (Mast, 1911, p. 224).

In light from two sources both Eristalis and Erax, go toward a point between the sources. The location of this point depends upon the relation of the luminous intensity of the light received from the two sources. The greater the difference the nearer the more intense illumination the point is located. When the insects are oriented in such a field of light the two eyes are not equally illuminated except when the light received from the two sources is equal. Consequently, when insects are oriented under natural conditions where they are nearly always subjected to light from various sources of unequal intensity, the eyes are rarely if ever equally illuminated. Under such conditions orientation is therefore not in accord with the Ray-Verworn theory as applied to insects by Bohn, Loeb, and others.

In specimens of Eristalis or Erax with one of the front legs removed orientation is practically normal. If such specimens are laterally illuminated they turn toward the light either to the right or to the left. If the front and the middle legs on the same side are removed, Eristalis deflects strongly toward the normal side, but after a few days it orients fairly accurately. Erax usually goes fairly directly toward the light at once, but only for a short distance after which it deflects rather sharply toward the normal side; then it ordinarily attempts to turn in the opposite direction, but it usually fails, and topples over. The movements of the legs are not well coördinated and there is consequently much difficulty in locomotion. Orientation in these specimens obviously can not be due

to equal action in locomotor appendages on opposite sides as the theory in question demands. Specimens of Eristalis with the front and middle legs on one side removed and either eye covered may under certain conditions proceed fairly directly toward the light. If the direction of the rays is changed while they are thus proceeding toward the light, they reorient by turning either to the right or to the left. This shows that the movements of the legs on either side may be controlled by impulses originating in either eye. These responses are obviously not in accord with any theory of orientation that demands balanced or equal action either in the receptors or in the locomotor appendages on opposite sides.

In certain fire-flies the male, in response to a flash of light produced by the female, turns thru the required angle, no matter in which direction he may be going in reference to the location of the flash, and proceeds directly toward her. Thus after momentary illumination, he may turn in the total absence of light in any direction, thru angles varying from 0 to 180 degrees; and this turning is, under many conditions, a response to the illumination of but one eye. It is consequently evident that it cannot be accounted for by any theory which demands balanced or equal illumination of receptors on opposite sides as the basis of orientation.

The facts presented above show that there are a number of phenomena of fundamental importance in the process of orientation in insects that are not in accord with the Ray-Verworn theory. How can these phenomena be explained?

Insects have image-forming eyes, so that when an eye is exposed to a source of light an image is produced on the retina, and if the source is concentrated the image is very small, resulting in definite localization of the stimulus. Thus while the whole surface of the eye is illuminated the stimulus may be confined to a minute portion of the retina, the location of which depends upon the location of the source of light in relation to the longitudinal axis of the insect. If the light is in front of the insect the image is near the anterior edge of the retina; if it is to the side the image is on the lateral surface of the retina, etc. In general it is always directly below the ommatidium whose longitudinal axis is parallel with the rays of light.

The flash produced by a female fire-fly forms on the retina of the male a minute luminous image so that the stimulation is practically confined to a point. This point varies in location from the posterior to the anterior edge of the retina depending upon the axial position of the male in reference to the female, and it also varies in a dorso-ventral direction. There is then for every axial position of the male a definite location of the stimulus in the eye. The fact that in response to a flash of light produced by the female, the male turns after the flash has disappeared until he faces the female regardless of the extent of turning required, indicates that momentary stimulation of a point on the retina sets up a series of turning reflexes,

and that the series set up varies in character and in extent with every point; so that if the point stimulated is located at the posterior edge of the retina the series of reflexes carries him through a large angle, the degree of turning in every case depending upon the location of the stimulus. Thus in the fire-fly orientation is the result of series of reflexes, the nature and extent of which is specifically related to the location of the stimulus. There is much evidence indicating that similar factors are involved in the process of orientation in other insects.

If in Eristalis or Erax with one eye covered the stimulus is localized at the posterior edge of the retina, the feet on one side move forward while those on the other move backward, the two front feet deflecting toward the side stimulated, the two hind feet from this side. If it is localized in the lateral portion both front feet move laterally toward the light, as do also the middle feet but to a less extent. If it is localized in the central part of the anterior surface of the eye the feet on both sides move forward and the insect does not turn. If it is localized at the antero-median edge it turns toward the covered eye.

This indicates that stimulation of a given region of the retina in one eye induces certain definite reactions in all of the legs on both sides, of such a nature as to tend to turn the insect toward the point stimulated just as it does in the fire-fly. But if there is only a momentary illumination Eristalis and Erax turn thru only a very small angle regardless of the location of the stimulus, whereas the fire-fly turns until it faces the source of light. However, if the illumination continues, then, as Eristalis or Erax turns, the image of the source of light on the retina travels forward and a continuous series of points extending forward in the eye become successively stimulated and the stimulation of each successive point induces reactions of such a nature as to produce turning toward the region stimulated and the result is continuous turning until the image reaches the anterior portion of the eye and the insect faces the light. Orientation is brought about by a series of reflexes (differential responses to localized stimulation) similar to the scratch reflexes in higher forms induced by stimulation of various points on the surface of the body. In photic orientation the nature of each series of reflexes depends upon the localization of the stimulus in the eye just as the nature of the scratch reflexes depends upon the localization of the stimulus on the surface of the body. This is what occurs if the stimulation is confined to one eye. If both eyes are simultaneously stimulated other processes are involved as is indicated in the following paragraphs.

If Eristalis is exposed to light from two sources at the same distance and equal in size and intensity and so arranged that the rays cross approximately at right angles at the place of exposure, it will turn until it faces a point half way between the two sources and then proceed toward

this point. If the two sources of light differ in intensity it will turn until it faces a point nearer the more intense source and the greater the difference the nearer this source the point will be. Under the first conditions the two eyes are equally illuminated when the insect is oriented; under the second they are not; the region stimulated in one eye is more intensely illuminated and it is farther forward than that in the other eye, and the greater the difference in the intensity of the two sources, the greater the difference in the location and in the intensity of the illumination of the regions stimulated in the two eyes. Consequently the turning effect of stimulation of a given region of the retina in one eye is obliterated by simultaneous stimulation of the same region in the opposite eye, provided the stimuli are of the same magnitude, and by simultaneous stimulation of any other region in the retina of the opposite eye provided the stimuli in the two eyes bear the proper relation in magnitude. If the stimulus in one eye is located relatively farther forward than that in the other eye, the former in order to produce complete inhibition, must be stronger than the latter, if farther backward it must be weaker.

The elimination of the effect of stimulation in one eye by simultaneous stimulation in the other eye is not due to antagonistic action of the legs on opposite sides as demanded by the Ray theory of orientation as applied to animals by Verworn, Loeb, Bohn, and others. The elimination is due to the total absence of any appreciable effect of the stimulating agent on the muscles of the legs. When an insect is oriented in light, the light has no immediate observable effect on the muscles.

Photic orientation in these organisms is the result of series of coördinated reflexes in the legs of both sides specifically related to the localization of the stimulus in either eye and inhibition or modification of the effect of the illumination in one eye by simultaneous illumination in the other.

This view of the process of orientation is in full accord with all of the phenomena presented above. It accounts for orientation in insects with one eye covered or with legs on one side removed as well as for orientation in normal specimens. It accounts for orientation on the wing in a vertical plane. It accounts for orientation in Caprella and in the fiddler crab. It accounts, moreover, for the facts observed by Dolley (1916) in Vannessa with one eye covered that the degree of deflection toward the functional eye in a horizontal beam of light is independent of the intensity, and decreases as the edge of the beam is approached where it becomes zero and that the degree of deflection may, in illumination from a concentrated source directly above, be greater in weak than in strong light, if reflection from the back ground is eliminated.

Photic orientation in insects is as a whole adaptive. It is rarely injurious except under unnatural conditions, as, e.g., in light produced by

a candle in a dark room. The reflexes resulting in orientation are similar to the scratch reflexes in the dog. How it is that they have come to be specifically correlated in character and extent with the localization of the stimulus in the eye is not known. They are instinctive in nature since they are largely independent of experience in the individual in which they occur and their origin is doubtless the same as that of other instinctive reactions.

A full description of photic orientation in Eristalis and Erax will be published shortly. This paper will contain an extensive bibliography including all of the literature referred to above.

HESPEROPITHECUS, THE FIRST ANTHROPOID PRIMATE FOUND IN AMERICA

By Henry Fairfield Osborn

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Read before the Academy, April 25, 1922

This communication to the National Academy, Tuesday April 25, 1922, was simultaneous with its publication in the American Museum *novitates.** A single small water-worn tooth, 10.5 mm. by 11 mm. in crown diameter, signalizes the arrival of a member of the family of anthropoid Primates in North America in Middle Pliocene time. The discovery is due to Harold J. Cook, consulting geologist, Agate, Nebraska.

The anthropoid Primate characters of the tooth are confirmed by another water-worn third upper molar previously found by William D. Matthew in the same beds but not described because it was not sufficiently distinctive. These two teeth establish the existence in the Pliocene period of a new and independent type of anthropoid, intermediate in the structure of its grinding teeth between the anthropoid ape and the human type. The animal is certainly a new genus of anthropoid ape, probably an animal which wandered over from Europe and Asia with the large south Asiatic element that has recently been discovered in our Pliocene fauna by Merriam, Gidley, and others. The generic name *Hesperopithecus* signifies *Pithecus* of the Western Hemisphere; its specific name *haroldcookii* is assigned in honor of the discoverer. The tooth actually resembles the human type more closely than it does any known anthropoid ape type; consequently it would be misleading to speak of this *Hesperopithecus* at present as like the known anthropoid apes; it is a new and independent type of Primate and we must seek more material before we can determine